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REPRODUCTION AND MORTALITY IN A POPULATION OF THE NORTHERN REDBACKED VOLE (CLETHRIONOMYS RUTILUS) AND THE MAIN FACTORS INFLUENCING THESE PROCESSES

Existing models of the numerical dynamics of terrestrial vertebrates (Tskipurishvili, 1966; Rubin et al., 1966) often are not representative of real populations and are unrealistic since they do not take into account fundamental natural interdependencies. From our point of view, good useful approaches require theoretical-mathematical and specific biological knowledge in order that one can use mathematical models for the description of specific species populations. Only in such a way is it possible to predict quantitative changes in numbers of animals resulting from the influence of man and natural factors. For the understanding and prediction of the processes of numerical changes and productivity of a population in the comtemporary scene, it seems to us that it is necessary to:

1) get a variety of quantitative characteristics of the processes of reproduction and mortality, which are comparable for various populations and species.

2) have an idea of the system, and order of entry into action, of population mechanisms determining an increase in numbers.

3) bring out how intra- and interspecific factors set in motion a process or influence its essential impact and determine the possibility of their quantitative expression.

Such materials permit the construction of models for the changes in numbers of populations, limited by the possible accuracy of our biological and logical-mathematical representations of the course of this process. This calls for work for several years on local populations, therefore small rodents are convenient for the analysis of the processes of the dynamics of numbers of populations. An example of this in large measure is the northern red-backed vole Clethrionomys rutilus Pall.-the "landscape" species of rodent in the Siberian taiga. A large amount of material has been accumulated on the biology of this species (Koshkina, 1965, 1967; Krivosheev, 1971; Revin 1973 and others).

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Materials on the red vole in the southern Kemerovski District, collected by a large association of zoologists over almost 20 years of observations (Okulova, Myskin, 1973), make possible an approach to creative models for the dynamics of numbers of this species. Knowing this, Koshkina (1967) established that the regulation of population numbers in this species in the Salair mountains consisted mainly in the proportion of young animals participating in reproduction. In similar work (Grozdov et al. 1972) we showed that the density of populations determines the significance of the subsequent density in the reproductive period in the Salair by 50-80% (determined monthly). At the same time it was noted (Okulova, Myskin, 1973) that initial population density was not solely influenced by factors which influenced numbers; meterological factors were also important, especially in the period of reproduction. Quantitative characteristics of the influence of factors were obtained.

The problem in its given form consists in determining the basic changes in reproduction and mortality from many years of material, as well as statistically using the influence of certain other factors and population density on these characteristics of populations of the red vole.

Materials used in this paper were collected from May to July 1961-1972 in the southern Kemerovski District- in the Salair mountains and in the western foothills of the Kuznetsk Alatau (Prokop'evski and Novokuznetski region). In the Salair mountains, work was conducted from 1961 to 1965, in 1961 in the neighbourhood of Novostroika, in 1962 in the neighbourhood of Tom'-Chumysh (also a small amount of work in 1963 & 1964), and in 1963-1965 in the neighbourhood of Tomsk. In the western foothills of the Kuznetsk Alatau (near Uskovo) work was conducted from 1966 to 1972. The zoologists V. A. Aristova and T. V. Koshkina, and university biology students from Moscow and Vladimir participated in the work. Descriptions by locality as to the methods and the extent of censusing of animals, and also the changes in numbers have been reported earlier (Okulova, Koshkina, 1967; Okulova et al., 1971; Okulova, Myskin, 1973). The number of animals was characterized by the percent capture in snap traps in the middle of the season (May-July) or in some months. Voles were dissected with the aim of determining reproductive condition and age. The age of voles was established both on the basis of the appraisal of the condition of internal organs (thymus, reproductive organs), and moult, and on the presence of roots in the upper molars (Koshkina, 1957). All voles were divided into overwintered, or old (having roots), and young of the year, or young (not having roots). Part of the work occupied a landscape of "low and midelevation black taiga", characteristic of the Altay-Sayanski mountain system. Despite certain local differences, these features were common to the general landscape. The Salair mountains were more favourable for red voles, being one of the optimal parts of the range. Where we studied in the region of the

foothills of the Kuznetsk Alatau, conditions were apparently somewhat worse; numbers of the species were less than in the Salair. Having characterized the numbers of voles from previous work (Okulova, Myskin, 1973), we considered 2 periods in their life: the period of minimum numbers (May), and the period of maximum numbers (July). The period of reproduction took place between these two dates, when in general the number of voles increased. From July to May of the next year reproduction did not take place, and the number of animals gradually decreased due to mortality.

NUMBERS AND SPECIFIC PARAMETERS OF REPRODUCTION IN THE VOLES

Table 1 gives the specific values for the numbers of the species in the critical periods of life for the studied populations. We have already reported a more detailed analysis of changes in numbers (Okulova, Myskin, 1973), in which we noted that the catch in snap traps per 100 trap nights varied in different years and various localities from 0.5 to 14.2 in May, and from 3.1 to 26.6 in July. These indices were higher in the Salair than in the foothills of the Kuznetsk Alatau. The realized increase in numbers in the reproductive period in both regions did not exceed a sixfold level. The fraction of young in the population during the reproductive season, as can be seen from the table, changed in years from 45 to 83.9%. Among the parameters of reproduction, the following were chosen:

1) fraction of reproducing females among young females (in numbers reproducing, taking the sum of individuals pregnant or having given birth), (* SEE END OF MANUSCRIPT)

2) number of litters in the season per female living till the end of July,

3) average litter size.

These parameters were separately calculated for overwintered and young females, and are given in Table 2. From our values and the ones given in Koshkina (1967); reproducing females vary from 0 to 65.5% of young females in various years. Old females living to the end of July could produce from 1 to 3-4 litters in the season, with an average of 1-2.6; and 1-1.6 for young females. Litters in old females consisted of 6.1 to 8.1 embryos on the average, and 4.9 to 6.5 embryos in young females. Therefore, we observed significant variation in the specific reproductive parameters from year to year.

In order to consolidate all of our data and to obtain the common characteristics of reproduction in the populations during the season, we decided to calculate the quantity of embryos produced by a studied population. An estimation of the production of embryos has been carried out by a number of authors (Koshkina, 1967; Panteleev, 1968; Smirnov, 1973; Revin, 1973). But, these calculations were related in general to a single reproductive female, and not to the whole population. In Bujalska (1970) we found

theoretical calculations for the quantity of young produced by an entire population of bank voles on a small island. That calculation is not appropriate for large-scale populations, the population size of which we certainly do not know. In the latter case, it is apparently more advisable to calculate the productivity of young per hectare. We calculated the number of embryos "captured" in the course of the season per 100 trap nights. Nikiforov (1963) has found a directly proportional relationship between the abundance per 100 trap nights and the abundance per hectare, which allows us to use a proportionality coefficient. Our observations confirmed this conclusion (Okulova, 1975). We estimated the number of embryos per 100 trap nights for old and young animals. Thus, first of all, the midseason catch per 100 trap nights of pregnant females was determined for each group in question. This index increased as a function of the midseason number of litters, calculated at the end of July, and the number of young to a litter. Data obtained separately for the two age groups of females were summed to obtain the average number of embryos produced by a female caught per 100 trap nights in each season. The mortality of mature females in the course of the season was not entirely taken into account, since it was assumed that all females produced the number of litters taken into account by the end of July. In reality few females live to this date, which produces a smaller number of litters. Therefore, we subsequently took advantage of another method, and calculated the productivity of each group separately for each month in the reproductive period. From this we found that it was impossible for one female to be pregnant twice in the course of one month. An error resulting from this assumption can result in an underestimate, but it is not very important to take into account those mature females which produce 4 litters by the end of the season.

The standard calculation for the data is shown in Table 3, and the obtained results in Table 4. From Table 4 one can see that the productivity in the course of the season in various populations consisted of 5.8 to 37.4 embryos per season per 100 trap nights, or approximately 20-150 per hectare. For each initial overwintered female, 1.3 to 5.8 embryos are produced in the season. Revin (1973) and Smirnov (1973) found significantly higher figures: 10-40 young per initial female in the season. For various methods of calculation, it is equally necessary to take into account the fact that conditions of life and reproduction in a population are apparently more stable in the south of Western Siberia, and mortality of animals is less. Under our studied conditions, the number of animals did not generally increase in the reproductive period (Tomsk 1963, Table 1), or increased by 2-4 times, rarely by 6 times (Uskovo 1968). Average data characterizing reproduction and losses in the studied populations of red voles is presented in Table 5. Data on survival is worked out next.

SIGNIFICANCE OF INITIAL POPULATION DENSITY AND OTHER FACTORS IN THE DETERMINATION OF REPRODUCTIVE PARAMETERS AND TOTAL PRODUCTION OF THE RED VOLE

To estimate the role of population density and the quantitative significance of reproductive indices we calculated correlation coefficients for these parameters with the level of May numbers (Table 6, Fig. 1-4). From Table 6 one can see that there exists a close correlation between initial population density and a significant majority of the parameters of reproduction. Statistically significant correlation coefficients consist of 0.63 to 0.86. In other words, these parameters were 40 to 74% significantly determined by initial density. In all the examined indices, two were not significant:

1) the average number of litters in old females towards the end of July,

2) litter size of young.

In addition, a weak relation between the litter size of young females and the quantity of litters may exist (Zejda, 1966); apparently the significance of this influence is stronger than initial population density. Since indices of population increase in the reproductive season, and the proportion of young females participating in reproduction, and also the proportion of young in the population, are inversely dependent, the average litter size of overwintered females is apparently dependent as a second order parabola with a maximum at a catch of about 2-4 per 100 trap nights (Fig. 1). (THIS IS OBVIOUSLY ABSURD, SM).

To determine the relationship of reproductive indices in the red vole with the numerical level of competing species- the red-grey vole Clethrionomys rufocanus and the root vole Microtus oeconomus, we considered average data from May to July. Statistically significant relationships of the abundance of both competitors were found only with one index- the fraction reproducing among young females. Apparently, high densities of the root and the red-grey vole, as well as high densities of conspecifics, operate to depress reproduction in young animals. On the whole there is a marked inverse dependence of the fraction reproducing among young red voles on the density of these two species (Fig. 3). This tells one that competitive relationships are apparently manifested in the reproduction of young females; the reproduction of old individuals does not depend on numbers of competitive species. Therefore initial density is not only influenced by the results of reproduction, as noted previously (Okulova, Myskin, 1973). The regulatory influence of initial density on the level of abundance apparently consists of changes not only in mortality, but in the significance of the most important parameters of reproduction. A comparison of the calculated production of embryos with initial numbers (Fig. 4) indicated that the quantity of young born to the population was strongly

related to initial density. In the studied region on the whole, the magnitude of population increase in the course of the season is by 83% determined by initial density (P=0.01). The correlation coefficient here is about 0.91, i.e. the relation is highly significant.

To introduce an interesting question, what is the significance of different age groups in the general production of young, and to what degree does production by young and overwintered females depend on initial density? Fig. 5 presents the relation between production of embryos in old females and initial density. It can be seen that in years of high numbers the contribution of old females to overall production increases. Overwintered females contribute higher production, the higher their numbers. Although the litter size of old females decreases at high densities in general, this does not decrease the production of old females. In the majority of cases in the studied region, overwintered females all basically breed. The quantity breeeding in the population in the season is 72% (P=0.05) determined by the mid season level of numbers of overwintered breeding females. Statistical significance is not displayed with the numbers of mature young females. The reproduction of young strongly depends on the level of initial density. Thus where high initial numbers are maintained, the role of young in reproduction is minimal. The significance of young production increases in years of a deep depression, under unfavorable conditions, when the number of overwintered individuals in spring is very small. Other aspects are also apparently manifested in the production of young. For example, from Table 4 it can be seen that in 1971, despite low initial density, old animals made up 95% of the breeding population. Participation in reproduction of young females of the red vole was sharply reduced because of high numbers of the red-grey vole and the root vole in 1971. Similar results have been obtained by Revin (1973) and Smirnov (1973); in our studied region (which may be considered optimal for the species) the fecundity of the population is significantly lower (1.3-5.8 per one initial female, but in the Yakutia- it is about 30, and in the Middle Sikhota-Alin, 11 to 42).

Summarizing the presented data on reproduction one can say that the reproductive strategy of the red vole under optimum conditions consists of an increase in numbers mainly accounted for by overwintered females, the production of which increases proportional to the initial density of the stock. The increase in density takes place through the production of young. Their role is particularly increased in years of depressed numbers. The fact that young generally breed under suboptimal conditions possibly lowers the fitness of the population since old individuals bear the influence of selection longer and are apparently less influenced by it than are young of the year. In suboptimal areas less specialization is generally favorable since the effects of external factors are strong, and the species is

adapted to other conditions (the locality and period where the species originated). In other words, low initial numbers being investigated under unfavorable conditions reduce births in particular with large ecological plasticity, which can be more significant than narrow specialization under suboptimal conditions.

MORTALITY IN RED VOLES

To analyze mortality we divided the life-cycle of voles into 4 periods: 1) embryonic, 2) first summer of life, 3) autumn-winter period and 4) second summer of life. Voles practically never live to a third summer.

EMBRYONIC MORTALITY was determined from the number of resorbing embryos (Table 7). In our data, the resorption of embryos was somewhat lower in the Salair than in the foothills of the Kuznetsk Alatau. On average 0.8% of all embryos perished in the Salair as opposed to 3.9% in the foothills of the Kuznetsk Alatau. Deaths were higher in old females. In general one can say that the level of resorption was insignificant.

Among the factors influencing embryo resorption we noted only the sum of temperatures in late spring - early summer (May-June).** In old females the resorption of embryos was higher, the colder the period. Particularly unfavorable years have May-June temperatures lower than 26°. The amount of resorption in these years is 7.08%, as compared with 1.05% overall. The correlation coefficient between the amount of resorption in old females and the sum of average monthly temperatures in May-June is 0.809 (P=0.01 for 10 points).

MORTALITY IN THE FIRST SUMMER OF LIFE sums nestling mortality and mortality during the active life of young animals. Some idea of nestling mortality can be obtained from marked grid data from 1963 (near Tomsk) and from 1967 and 1970 (near Uskovo). At the end of May in 1963, 29 overwintered red voles inhabited the marked grid in fir forest. From live and dissected animals captured in the neighborhood of the plot we know that all old females reproduced, producing one litter of about 7.9 young by that date. Consequently one would expect to capture about 229 young animals towards the beginning of July. We actually caught 28. Hence, losses (mortality + emigration) were 87.8% for the first litter. The corresponding calculation of losses for animals in 1967 on the plot in fir forest was 77%. On the same plot in 1970, old females in May ought to have given birth to 63 young. We marked only 25 young towards the beginning of June on the plot, or 39.5% of the expected numbers, representing losses of 60.5%. Therefore nestling mortality of young is probably 60 to 80% of those produced. The mortality index may be somewhat dependent on the inclusion of migrants, but one must note that the considered years (1963, 1967, 1970) were peak years, when

the number of migrant animals was relatively small. Given this assumption, migratory characteristics of young are expressed at an older age. Mortality of young after leaving the nest can be determined from the disappearance of marked animals during the period of marking. Naturally this calculation also includes migrant animals. In 1963, 93% of 28 marked young animals survived from the end of June to the end of July; similarly, 55.8% of 34 survived in 1967. In 1970, 56% of 25 young marked in early June survived to the end of July, and 86% of 50 young alive in the second half of June survived through one month. *** From these results it appears that post-nestling mortality is significantly lower than nestling mortality: from half to all of the mass of young recruited survive to the beginning of August. Furthermore, we calculated mortality of young animals by comparing data on the production of embryos with captures of young animals in snap-traps in July (Table 4). From the table one can see that survival varies from 26.2% to 72% in the first summer of life, i.e. 1/3 to 2/3 of the animals die.

Survival of young during the first summer of life is not significantly determined by initial density. We discovered that survival of young, as in the resorption of embryos in old females, was significantly related to early summer temperature (May-June): the warmer the beginning of the summer, the higher the survival of animals. Given a sum of temperatures in the period up to 25.5°, survival was 26-30% in young, and given a sum of 27.6° and higher, survival was 43-72% in young. The strength of the influence of this factor in influencing survival was 64% (P=0.05), given a correlation coefficient of r=0.80.

MORTALITY IN THE AUTUMN-WINTER PERIOD was considered in an earlier paper (Okulova, Myskin, 1973). From those data we found that about 1/3, but sometimes more, animals survive through winter.

MORTALITY OF VOLES IN THE SECOND SUMMER OF LIFE. On the plot in 1963, 20.4% of 54 overwintered red voles survived from the end of May to the end of July; similarly 59% of 17 voles survived in 1967. In 1970, 84% of 25 marked overwintered animals survived from the first half of June to the end of July, In agreement with these dta, old voles survived much better in the second summer of their life in the Kuznetsk Alatau in 1967 and 1970 than in the Salair in 1963. The level of mortality in live-caught overwintered animals can also be compared with captures in snap-traps in May and July. These data show that the survival of old voles to July was usually rather good: half of the time all of the animals survive, and only in about 1/3 of the cases did less than 1/3 survive. Average mortality in these cases over a 10-year period was 29.6%.

We did not detect a relationship between survival in the second summer of life and initial or midseason density.

At the same time we also found that survival of overwintered animals from May to July was significantly higher in years with a warm spring and beginning of summer (sum of average monthly temperatures in April-June). When temperatures were 31° or higher numbers of old animals did not decrease from May to July; and when temperatures were less than 26° no more than 1/3 of the old animals survived. The correlation coefficient calculated between the survival of animals in their second summer of life and the sum of temperatures from April to June from 1963 to 1972 was 0.757 (P=0.05). In other words, survival of voles in this period is 57.3% determined by the effects of spring-summer temperature. This figure increases to 79.1% (P=0.05) if the calculation for 1972 is excluded, a year when survival of voles was unexpectedly low. Additional harmful competitive factors may have influenced herbivorous voles, the red-grey vole and the root vole, which were half as numerous in 1971 and 1972 (during all the life of the specified generation). Using all of the available data, we graphed population numbers of the red vole in the studied region in the course of the season, taking into account the effects of reproduction and mortality, and the effects of varying survival with age (Fig. 6). From this figure and previous statements, it is clear that the most intense losses occur in young animals in the first summer of life, subsequent survival is much higher, losses are not so intense. In conclusion, processes of reproduction are significantly related to observed initial population densities of the species, and to a lesser extent of competitive species, whereas survival (mortality) in all periods of life depends to a large extent on environmental conditions and not on density.

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* Okulova has not mentioned anything about adjusting calculations for females that are pregnant but have no visible embryos (except for the comment on including parous females in the calculation). Her estimates are therefore probably too low by a factor of 1/2 to 2/3.

** References to temperature variables in this paper are obscure. Okulova appears to have added together average temperatures (max or min?) over either a two or three month period, hence the unusually high values reported for temperatures.

*** The data for 1970 are confusing since Okulova talks about recruitment in early June in one case and then talks about recruitment later on in the month as well. Reproduction presumably started earlier in this year.

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REPRODUCTION AND MORTALITY IN A POPULATION OF THE NORTHERN REDBACKED VOLE *(CLETHRIONOMYS RUTILUS)* AND THE MAIN FACTORS OF THESE PROCESSES

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Summary

The materials on reproduction and mortality of the northern redbacked vole in the south of the Kemerovo District in 1961—1972 are given. It has been shown that the majority of youngs in this region of the range optimal by its conditions is produced by the overwintered animals. The production of youngs in the population is by 89% determined by the initial density. The intensity of reproduction of the overwintered females is controlled by the initial density of adults and that of females-youngs of the year by the initial density of not only its own species but also other species of rodents. The mortality of voles is the highest during the earliest periods of life (after birth). The mortality during the life depends, mainly, on meteorological factors.

Table 1. Numbers, increase, and composition of the population in the red vole.

Area	Year	% Captures MAY	% Captures JULY	Increase July / May	Animals Captured May to July	
					Total	% Young
Novostroïka	1961	3,6	16,0	4,45	—	—
	1967	7,8	20,5	2,62	—	45,0
Tom'Chumysh	1962	1,8	10,2	5,69	—	—
	1963	8,4	16,5	1,96	239	47,5
	1964	3,0	14,4	4,80	272	73,0
Tomsk	1963	14,2	14,0	1,00	1942	53,2
	1964	2,8	7,8	2,79	764	83,0
	1965	10,1	26,6	2,62	2335	46,4
Uskovo	1966	1,0	4,2	4,20	438	73,6
	1967	2,9	10,1	3,49	596	64,8
	1968	0,5	3,1	6,0	343	74,1
	1969	2,0	10,9	5,45	510	60,3
	1970	3,8	9,5	2,50	624	70,9
	1971	1,8	7,9	4,40	211	55,2
	1972	2,7	5,4	2,0	292	83,9

Table 2. Indices of reproduction in the red vole.

Area	Year	Fraction Reproducing Among Young ♀♀		Mean # litters towards the end of July				Mean # embryos per pregnant female			
				Overwintered		Young		Overwintered		Young	
		All ♀♀	%	All ♀♀	litters	All ♀♀	litters	All ♀♀	# embryo	All ♀♀	# embryos
Novostroïka	1961	—	—	—	—	—	—	163	7,2	41	6,3
	1967	—	—	—	—	—	—	17	6,8	2	6,0
Tom'Chumysh	1962	—	—	—	—	—	—	—	5,7	—	4,9
	1963	75	1,3	—	—	—	—	44	6,1	—	—
	1964	90	57,9	—	—	—	—	15	7,6	31	5,7
Tomsk	1963	304	2,0	40	1,8	—	—	157	6,7	—	—
	1964	273	58,0	9	2,4	34	1,0	39	7,4	88	5,5
	1965	361	12,8	44	2,1	59	1,1	145	7,4	39	5,8
Uskovo	1966	137	51,0	11	1,5	59	1,2	24	6,7	48	6,1
	1967	174	26,5	20	1,8	24	1,3	45	6,7	18	6,2
	1968	134	46,6	14	2,1	31	1,6	12	7,0	34	5,9
	1969	160	34,3	32	2,2	49	1,2	43	6,9	31	6,3
	1970	230	62,5	22	2,6	67	1,5	34	7,7	39	5,7
	1971	53	5,7	13	2,1	1	1,0	16	6,8	2	6,0
	1972	85	65,9	5	1,0	26	1,2	10	8,1	27	6,5

Table 3. Example of the calculation of embryo production in the population of the red vole (per 100 trap nights)

Area	Year	Month	CATCH PER 100 TN OF ALL MATURE ANIMALS	% of females pregnant in the population		CATCH PER 100 TN OF PREGNANT FEMALES		Mean number of embryos recorded in		Embryo production in the season		Sum of Population Production
				OLD	YOUNG	OLD	YOUNG	OLD	YOUNG	OLD	YOUNG	
Tomsk	1963	Май M	14,2	20,6	—	2,92	—	7,9	—	23,0	—	23,0
		Июнь J	12,5	16,2	—	2,02	—	6,7	—	13,7	—	13,7
		Июль J	14,4	4,0	0,3	0,58	0,04	5,5	5,0	0,29	0,2	0,31
		Август A	19,0	1,9	—	0,04	—	5,0	—	0,18	—	0,18
		За сезон (Total)								37,17	0,2	37,4
Uskovo	1966	Май M	1,02	37,5	—	0,38	—	8,0	—	3,05	—	3,05
		Июнь J	2,47	9,3	7,95	0,23	0,20	6,7	6,5	1,54	1,30	2,84
		Июль J	4,06	2,4	17,1	0,10	0,69	7,4	6,0	0,74	4,15	4,89
		За сезон (Total)								5,33	5,45	10,78
	1970	Май M	3,8	34,2	—	1,30	—	9,0	—	11,7	—	11,7
		Июнь J	7,85	6,67	5,6	0,52	0,44	7,8	6,5	4,05	2,85	6,9
		Июль J	10,80	2,86	8,9	0,31	0,96	6,2	5,41	1,90	4,30	6,2
		За сезон (Total)								17,65	7,15	24,8

Table 4. Production of embryos in the red vole (per 100 trap nights), increase, and survival of young

Area	Year	CATCH PER 100 TN MAY	Production of embryos per 100 trap nights by females			% of Overwintered females participating in reproduction	Increase relative to initial numbers		Survival of Young
			Overwintered	Young	Total		Possible	Realized	
Tom' Chumysh Central Salair	1963	8,4	27,4	—	27,4	100,0	3,4	1,96	36,5
	1964	2,3	6,69	11,2	17,9	37,5	7,8	4,8	53,0
Tomsk	1963	14,2	37,17	0,2	37,4	99,5	2,62	1,00	31,0
	1964	2,8	5,59	17,11	22,7	23,6	8,15	2,79	45,1
	1965	10,1	27,1	7,0	34,1	79,5	3,45	2,62	72,0
Uskovo	1966	1,02	5,33	5,45	10,78	50,2	10,3	4,2	32,2
	1967	2,83	17,41	3,78	21,19	82,0	7,80	3,19	35,0
	1968	0,5	2,12	3,66	5,78	36,9	11,6	6,0	41,7
	1969	2,0	10,81	6,07	16,88	64,0	8,44	5,45	43,0
	1970	4,25	18,95	7,15	26,1	72,5	6,15	2,50	30,6
	1971	1,8	13,41	0,72	14,13	95,0	7,95	4,40	36,6
	1972	2,7	10,89	8,05	18,94	57,9	7,0	2,0	26,2

Fig. 1. Influence of the level of initial density on litter size in overwintered red voles. (x1- abundance of red voles per 100 trap nights in May, y1- litter size in overwintered females)

Fig. 2. Influence of the initial density (x1) on seasonal increase (y') and % young (y'') in populations of the red vole.

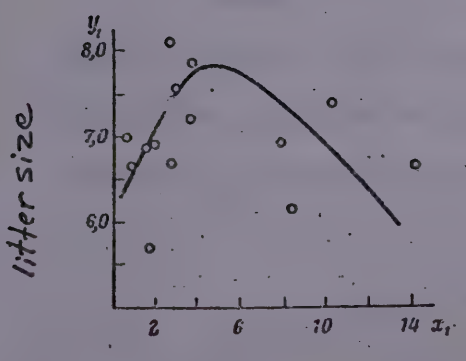
Fig. 3. Influence of the level of midseason abundance of 3 species of rodents on the fraction reproducing among young females of the red vole (x2- midsason abundance of the red vole per 100 trap nights, x3- same for the red-grey vole, x4- same for the oeconomus vole, y- fraction of animals participating in reproduction among young females of the red vole)

Fig. 4. Influence of the level of initial density on the embryo production of the population. (y- number of embryos produced per 100 trap nights, x1- abundance of the red vole per 100 trap nights in May)

Fig. 5. Relationship between embryo production per 100 trap nights over the season by overwintered females and initial density. (y- production, x- density)

Fig. 6. Level of mortality in the red vole in various periods of life. (x- age of voles in months, a- 1st summer of life, δ-autumn-winter period, ß - 2nd summer of life, y- % left alive)

(1)



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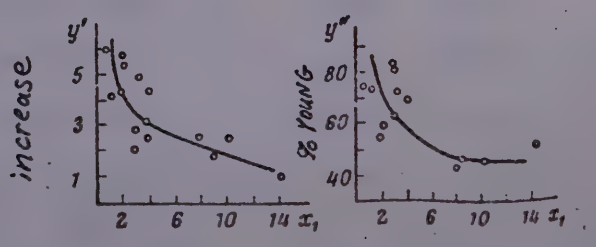
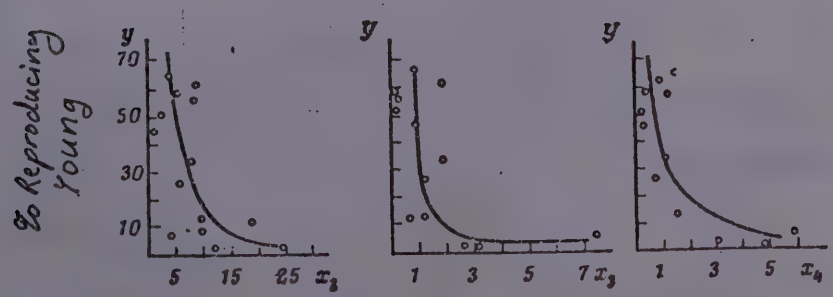


May catch C. rutilus

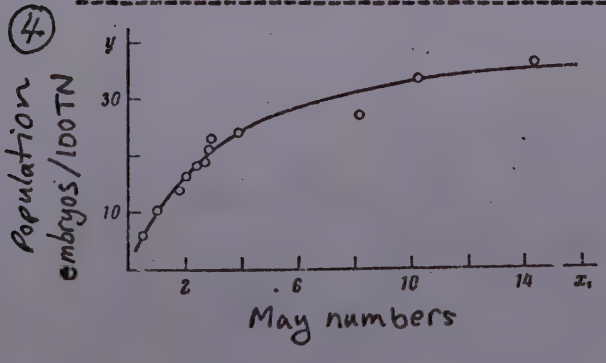
(3)

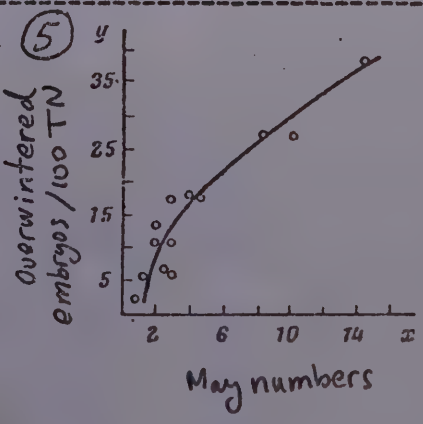


midseason catch C. rutilus C. rufocanus M. oeconomus

Table 5. Parameters of numbers, reproduction and mortality in the red vole in the Southern Kemerovski District (1961-1972).

Index	Range	Mean
Numbers in May (per 100 trap nights)	0.5-14.2	4.4
Numbers in July (per 100 trap nights)	3.1-26.6	11.8
Realized increase in population in the reproductive season	1.0-6.0	2.7
Fraction reproducing among young females	0-0.66	0.353
Average number of litters in the season		
Overwintered	1-2.6	1.96
Young	1-1.6	1.23
Average litter size in the season		
Overwintered	5.7-8.1	6.7
Young	4.9-6.5	5.9
Production of embryos in the season		
per 100 trap nights	5.8-37.4	21.11
per initial female	1.3-5.8	3.5
Resorbing embryos (% dead of all embryos)		
Overwintered	0-13.6	3.9
Young	0-2.8	1.0
Survival of young in 1st summer of life (%)	26-72	40.6
Survival in the autumn-winter period (%)	5-100	38.2
Survival in 2nd summer of life (to July) (%)	23-100	70.4





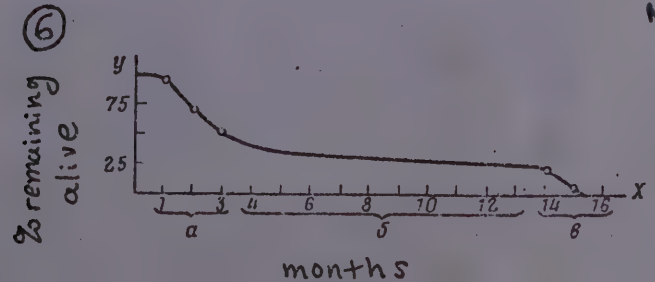
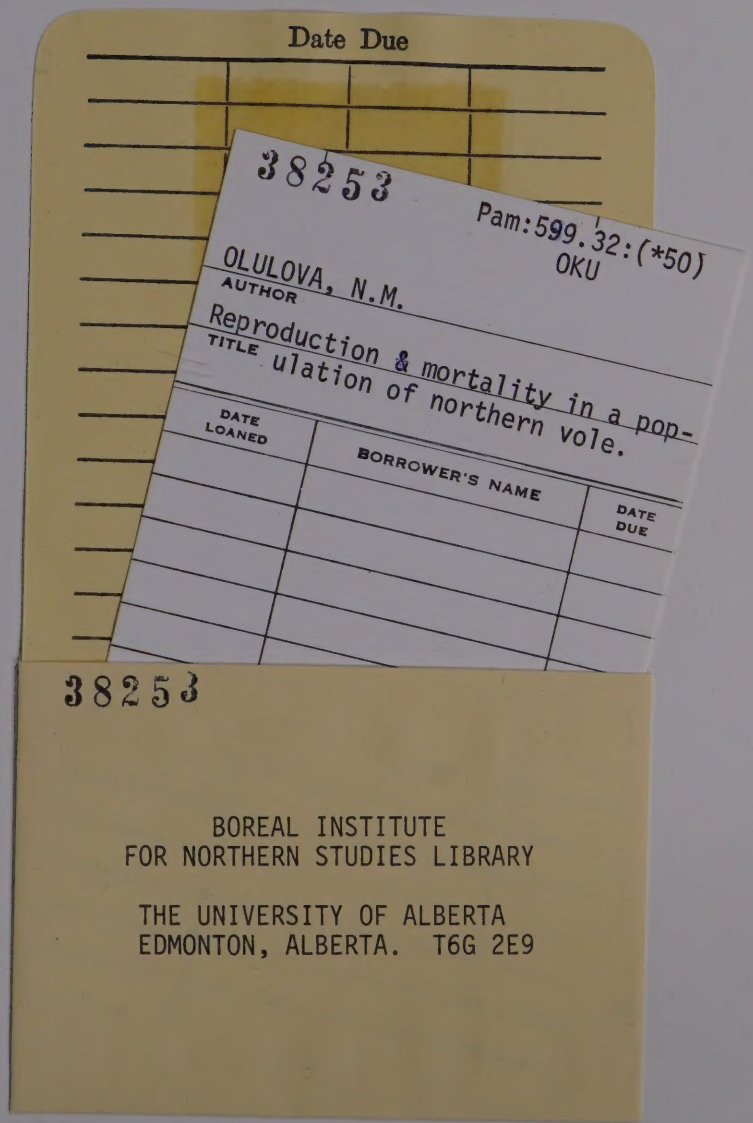


Table 6. Relationship of the indices of reproduction and the composition of the population of red voles with initial (May) and midseason numbers.

Influencing Factor	Index Dependent on Numbers	r^2	Prob.
May numbers of the red vole	Increase in the season of reproduction	0.400	0.050
	Proportion participating in reproduction among young females	0.590	0.001
	Number of embryos in litters of overwintered females	0.539	0.050
	Proportion of young in the population	0.742	0.010
Midseason numbers of the red vole	Proportion of young in the population	0.653	0.010
Midseason numbers of the red vole	Proportion participating in reproduction among young females	0.602	0.001
Midseason numbers of the red-grey vole	"	0.681	0.001
Midseason numbers of the oeconomus vole	"	0.601	0.001

Table 7. Resorption of embryos in the red vole.

Area	Year	Overwintered		Young	
		% Resorbing	# embryos	% Resorbing	# embryos
Tomsk	1963	0,6	1438	—	—
	1964	1,2	323	1,04	666
	1965	0,7	1331	1,8	381
Uskovo	1966	1,9	160	2,7	293
	1967	2,6	301	0,0	111
	1968	0,0	84	1,0	200
	1969	1,85	268	0,51	195
	1970	1,14	261	0,0	223
	1971	6,5	108	0,0	12
	1972	13,6	81	2,8	176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